Running head: EEG COHERENCE, AGING, AND MEMORY

Electroencephalographic coherence, aging, and memory: distinct responses to background context and stimulus repetition in younger, older, and older declined groups.[1]

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Abstract

The current study examines the EEG coherence of young, old, and old declined adults performing a visual paired associates task. In order to examine the effects of encoding context and stimulus repetition, target pairs were presented either on detailed or white backgrounds and were repeatedly presented during both early and late phases of encoding. Younger adults were found to have lower levels of frontal-temporal and temporal-parietal coherence, but higher levels of frontal-parietal coherence, particularly for the gamma frequency band. A number of differential coherence responses to background context and early versus late encoding phases were also observed across the groups, particularly for lower alpha and upper alpha frequencies. Coherence-performance maps were generated to further explore topographical differences in the relationship between coherence and performance across groups. Results revealed a more diffuse pattern of negative coherence-performance relations in older declined adults. Results are discussed in light of the literature on age-related cognitive decline.

Older adults appear to have more difficulty than young adults when it comes to placing remembered events into the appropriate context with respect to time and place (Craik & Jennings, 1992; Friedman, 2000). The term context is quintessentially adopted to refer to spatial, temporal or cognitive information that is present in the environment and surrounds the memory task target but is irrelevant or at most incidental to the cognitive task being performed. The association between viewed items and the context in which they appear has been termed contextual binding (Mitchell, Johnson, Raye, Mather, & D'Esposito, 2000). Prior research has established that contextual details are bound to item information (Chalfonte & Johnson, 1996), and facilitate object identification (Biederman, Mezzanotte, & Rabinowitz, 1982).

Howard et al. (2006) proposed that the hippocampus is responsible for binding items to the contexts in which they are presented. FMRI studies have offered evidence of hippocampal dysfunction associated with memory decline in the elderly (Small et al., 1999). However, less is known about the electrophysiological correlates of contextual binding in younger and older adults. A number of electrophysiological studies have pointed to changes in both frontal and parietal activations being associated with memory decline in older adults (Gutchess, Ieuji, & Federmeier, 2007; Lawson, Guo, & Jiang, 2007; Wolk et al., 2009). Lawson, Guo and Jiang (2007) found that older adults had poorer working memory performance as well as a lower level of frontal scalp electrical activation in comparison to younger adults. Wolk et al. (2008) used EEG to examine age-related changes in item recognition memory, finding that early frontal area activity was markedly lower for the poorer-performing older group. Gutchess, Ieuji and Federmeier (2007) compared young and old participants' abilities to recall a scene from memory, finding that recognition levels were unaffected by age, but that the older groups showed lower activations than younger adults in frontal and parietal areas.

Importantly, the distributed brain activation patterns of younger and older adults can differ in response to similar task demands. For example, as described by the HARLOD (hemispheric asymmetry reduction in older adults) model, when compared with younger adults, older adults show a reduction in asymmetrical activation of the frontal cortex during verbal recall (Cabeza, 2002). Some research suggests that these findings represent compensatory recruitment of neural reserves in older adults (Reuter-Lorenz et al., 2000). For example, Reuter-Lorenz and colleagues found that greater bilateral activity was associated with better memory performance in older adults, but not younger adults. Nevertheless, further research is needed to understand how the distributed brain activation patterns of younger and older adults impact upon contextual binding and the consolidation of new memories.

One electrophysiological analysis strategy that may shed light on the distributed brain activation patterns that moderate contextual binding problems and memory decline in older adults is coherence analysis. Coherence between two EEG signals, which is the squared cross-correlation in the frequency domain between two EEG time series measured simultaneously at different scalp locations (Nunez, 1981), has been interpreted as a measure for the degree of synchronization between brain signals of certain brain regions. Research suggests that patterns of high coherence between EEG signals recorded at different scalp sites have functional significance and can be correlated with different kinds of cognitive information processing, like memory, language, concept retrieval and music processing (Basar, Demiralp, Schurmann, Basar-Eroglu, & Ademoglu, 1999; Krause, Gibbons, & Schack, 1998; Petsche, Etlinger, & Filz, 1993; Petsche, Kaplan, Stein, & Filz, 1997; Schack, Grieszbach, & Krause, 1999; Weiss & Rappelsberger, 1998, 2000). In relation to memory processes, studies in healthy humans (Beaumont & Rugg, 1979; Krause et al., 1998; Sarnthein, Petsche, Rappelsberger, Shaw, & Stein, 1998; Weiss & Rappelsberger, 2000) have generally reported an increase of synchronization between brain regions involved in the respective task. In normal adults, interhemispheric coherence at rest decreases with advancing age (Duffy et al., 1996; Knott and Harr, 1997; Kikuchi et al., 2000). Studies comparing normal older adults to patients with AD have reported further reductions in interhemispheric alpha band (8–12 Hz) coherence between occipital sites (Anghinah et al., 2000) and in temporo–parieto–occipital areas in AD (Locatelli et al., 1998).

Coherence differences between younger adults, older adults, and cognitively declined older adults may vary as a function of task demands or features of stimulus processing. Hogan et al. (2003) observed a reduction in temporal-frontal coherence in upper alpha during a working memory task in patients in the early stages of Alzheimer's disease when compared with older adult controls. At the same time, Jiang and Zheng (2006) found that, compared with old controls, older adults with mild cognitive impairment (MCI) showed significant increases in inter- and intra-hemisphere coherence across all frequencies as task difficulty increased in a working memory task. Research also suggests that learning can result in a reduction in coherence. For example, Busk and Galbraith (1975) observed a decrease in coherence between premotor (FZ) and motor (C3 and C4) areas and premotor and occipital areas after practice on a hand-eye tracking task. Deeney et al. (2009) found that, when compared with novices, experts in visuomotor performance exhibit not only better performance but also lower levels of coherence between distributed cortical regions.

Notably, although past research has demonstrated age-related decrements in contextual binding (Chalfonte & Johnson, 1996), no study to date has examined coherence differences between younger and older adults in response to manipulations of encoding context, or the relationship between coherence during encoding and subsequent memory performance. The current study used a high density 64-channel EEG array to examine coherence during a visual paired-associate (VPA) learning task in 3 groups: younger adults, older adults, and older adults (matched on age and education) who scored 1SD below their peers on standardized tests of memory performance. The unique aspect of this study involved the presentation of different contextual backgrounds with each target pair. During the encoding phase, half of the visual paired associates were presented with a rich contextual background (i.e., colourful landscape) and the other half were presented without a background (i.e., white background). Participants were given no explicit instructions to memorise these detailed backgrounds. Furthermore, stimuli that were the focus of learning were presented a number of times throughout the encoding phase. This allowed us to examine repetition effects for both context rich and context poor stimuli. In the recognition phase, pairs of images were presented to participants either with or without a rich contextual background and were presented either in ‘congruous’ or ‘incongruous’ form (i.e., with or without the original encoding context). The current study examined, first, whether or not there are different physiological responses to context rich versus context poor stimuli across three groups, and whether or not physiological differences between context rich and context poor stimuli alter as a result of stimulus repetition during encoding.

In light of research demonstrating reductions in interhemispheric lower and upper alpha band coherence associated with normal ageing and age-related cognitive decline (Anghinah et al., 2000; Locatelli et al., 1998; Hogan et al., 2003), we hypothesized reduced alpha coherence in old declined adults relative to younger adults and older controls. In light of research demonstrating that older adults have more difficulty than younger adults recalling the encoding context of remembered events (Jennings & Jacoby, 1997), we hypothesised that context reinstatement effects would be largest in younger adults and smallest in the older cognitive declined group. Furthermore, when compared with young and old controls, we hypothesised older cognitive declined adults would show a less significant coherence difference between context rich and context poor pairs during encoding, and a less significant coherence difference in response to repetition of stimuli, particularly in both the lower and upper alpha frequency bands, which are known to be sensitive to the effects of ageing and to be associated with both effortful attention and the processing of semantic information, respectively (Klimesch, 1999). At the same time, in light of research from both human and animal studies supporting a role for neuronal synchronization in the gamma band underlying feature binding, learning, and memory (Herrmann, Fründ, & Lenz, 2010; Jensen, Kaiser, & Lachaux, 2007; Rieder, Rahm, Williams, & Kaiser, 2011), we also hypothesized that group and stimulus differences would be observed in gamma coherence.

In addition to an analysis of group and stimulus differences in coherence during encoding, we also examined the relationship between coherence during the early and late stages of encoding and subsequent memory performance in the younger, older control, and older declined groups, respectively. Although some research points to reductions in coherence associated with skill development (Busk & Galbraith, 1975; Deeney et al., 2009), coherence changes associated with learning and memory are most likely dynamic and non-linear, in the sense that both positive and negative coherence-performance relations emerge and dissolve as different neural networks or assemblies are established and disestablished. This view is consistent with the framework and research findings of Silberstein, Neuper, & Klimesch (2006), who describe a process of "functional connectivity sculpting". Specifically, Silberstein and colleagues found that functional connectivity changed dramatically over the time course of a mental rotation trial, with a largely negative coherence-performance relation observed during the encoding of objects, a mixture of negative early-stage and positive late-stage coherence-performance relations observed during a retention phase, and largely negative coherence-performance relations emerging again during the mental rotation phase of the task. Silberstein argued that performance ability is related to a capacity to strengthen coherence between cortical regions that are relevant to current cognitive demands while attenuating irrelevant connections, and thus patterns of coherence-performance relations change as cognitive demands change. In the current study, we explored the possibility that group differences in both negative and positive coherence-performance relations reflect differences in the way in which younger, older, and older declined adults establish synchronous connections between cortical regions that are relevant to current cognitive demands and subsequent memory performance. More specifically, evidence for the HAROLD model suggests that age-related hemispheric asymmetry reductions may have a compensatory function or they may reflect a dedifferentiation process (Cabeza, 2002). Consistent with the HAROLD model, we explored the possibility that, relative to older adults, better memory performance in younger adults would be associated with a smaller set of positive and negative coherence-performance relations (i.e., a more differentiated functional network). We also hypothesized that older cognitively declined adults would have the largest set of coherence-performance relations associated with better memory performance. While current theory and research suggests that gamma synchronization may be more critical than other frequencies during the formation of new neural assemblies that undergird associative learning, theta is known to be involved in memory processing and has been related to gamma (gamma appearing during particular phases within the theta cycle) in studies using intracortical recordings (Mormann et al., 2005), and EEG recording (Demiralp et al., 2007). Furthermore, both gamma and alpha modulation have been reported in studies of working memory, where alpha has been related to both memory and active inhibition (Jokisch & Jensen, 2007). Therefore, in order to better understand the influence of gamma coherence relative to other frequencies in the context of coherence-performance relations, the current study examines coherence-performance relations across groups and stimulus conditions in the theta, alpha, and gamma range.

Methods

Participants

19 young, 17 old, and 15 old who performed 1 SD below age- and education matched peers (Mean age = 21.3, 73.6 and 71.9 years; Education = 15.8, 12.9, 12.5 years, respectively) were recruited with informed consent. All participants received a comprehensive medical and neuropsychological assessment (Hogan et al., 2003; Swanwick et al., 1996). Participants were all non-smokers, right handed, native English speakers, and did not have medical conditions and were not on medication that affected the CNS. Participants were also screened for diabetes and head injuries. The study was approved by the NUI, Galway ethics committee and was carried out along the principles laid down in the Helsinki Declaration.

Neuropsychological Assessments

Medical/neuropsychological and electrophysiological/information processing assessments took place on two separate days. On the first day neuropsychological screening tests were conducted to evaluate the memory and cognitive function of participants. Individuals were excluded if they were smokers or if they were taking medication with CNS-effects. Also excluded were left-handed people, those who did not speak English as a first language, and those with epilepsy, diabetes, or a history of head injury, strokes or transient ischemic attacks (TIAs). Those with a history of depression but who were currently not affected were considered for inclusion, as were those who had thyroid problems or hypertension which had been stably controlled for three months or more. Neuropsychological screening tests included: the mini-mental state exam (MMSE), a memory self-rating scale, the hospital anxiety depression scale (HADS), the national adult reading test (NART), a test of fluency (animal naming), the word reading subtest of the Wide Ranging Achievement Test (WRAT), the Stroop task, and three subscales of the Wechsler Memory Scale (WMS; Logical Memory, Faces and Visual Reproduction) (see table 1).

Insert Table 1 around here

To allocate older adults into the `normal' and `declined' groups, scores on the three subscales of the Wechsler Memory Scale (WMS; Logical Memory, Faces and Visual Reproduction) were used. Scores on these indices were compared to scores on the national adult reading test (NART). Scores on the NART provide an estimation of premorbid IQ (Baltes, 1997). Older adults were placed in the `normal' group if their WMS memory score was not more than 1SD lower than their NART score, and allocated to the `declined' group if their memory score was 1SD or more below their

NART score. This system of measurement allowed for the identification of those older adults whose memory function was in the early stages of decline relative to age- and education-matched peers.

The number of years in formal education was significantly larger in the younger group compared with the two older adult groups. There was no difference between the three groups on the NART. Young adults scored higher than both old adult groups on the three sub-scales of the WMS ($p = .001$ for all six comparisons). Older controls scored significantly higher than the older declined group on the logical memory sub-scale ($p = .01$).

EEG Task

During the second day's session participants were prepared for the EEG recording and provided with an opportunity to practice the task. The visual paired associates task had both an encoding and recognition phase. During the encoding phase participants were presented with 12 pairs of abstract, non-verbalisable stimuli on screen for 3500ms, with an inter-stimulus interval of 1750ms. Six of the pairs were presented on a white background (no context) and six were presented on a detailed background (context; colourful landscape). Each pair of stimuli was presented six times, three times during the earlier stage of encoding and three times during the later stage of encoding (early / late), yielding a total of 72 trials in the encoding phase. Participants did not have to make any responses during the encoding phase. They were instructed to try to remember which stimuli formed pairs, and to ignore the background.

The recognition phase, which was presented immediately afterwards, required participants to respond to stimulus pairs that appeared on screen and make judgements about whether the two stimuli had been presented together in the encoding phase (a `true' pair - green button) or whether they had not previously been paired (a `false' pair - red button). One half of the pair was presented alone for 1000ms and was followed by the second, which lasted on screen for a maximum of 3500ms. The pair disappeared upon the participant's response. A total of 192 pairs appeared in the recognition phase. The background present during the encoding phase, either detailed or white, was either reinstated or not during the recognition phase (congruent vs. incongruent trials; see Figure 1).

Insert Figure 1 around here

EEG Recordings

Electrophysiological data were recorded in AC mode with a gain of 500 and a band pass of 0.5 and 100 Hz. The A/D conversion rate was 1000Hz. Each participant wore an ActiCAP EEG recording cap connected to the BrainVision EEG recording system. Scalp potentials were obtained using a 64-channel array with a common reference electrode and an anterior scalp ground (Afz). The electrode array conformed to the International 10-20 System. Vertical eye movements were recorded with two electrodes placed above and below the left eye, while electrodes at the outer canthus of each eye recorded horizontal movements. Silver/silver-chloride (Ag/AgCl) electrodes were used at all sites. Recording commenced when electrical impedance had been reduced to less than 10kOhms. Triggers identifying the type of stimulus presented were sent via the amplifier to the EEG recorder upon their presentation in E-prime. Triggers were also sent identifying participants' responses and the timing of the response.

Behavioural data processing

Hits, misses, false alarms, and correct rejections were calculated in SPSS and d' (discriminability index) scores, based on signal detection theory (STD; Thomas, 2002), were computed for each participant as a marker of overall performance. To calculate d’ the following formula was used

$$d' = z(\mathrm{H}) - z(\mathrm{FA})$$

where z is the z-score, and FA and H are the False Alarm and Hit rates, respectively.

Electrophysiological Data Analysis

Bad channels caused by faulty connections were deleted manually from the continuous EEG recordings. These recordings were then subjected to ocular artifact reduction using blink-averaging algorithms to remove artifactual scalp potentials caused by eyeblinks. Sweeps in which amplitudes exceeded 100 mV at any scalp electrode were automatically rejected. All sweeps were baseline corrected using the prestimulus interval as the baseline interval and epoched into single sweep recordings, from -250ms prestimulus to 1000ms post stimulus. Incorrect responses and non-responses were manually selected from these EEG sweeps and were excluded from the subsequent analysis. The remaining epochs were separated into stimulus categories. The linear coherence metric was calculated using 512 point (i.e. 512 ms duration) Hanning windowed versions of the EEG channel samples, by applying this frame coherence analysis to 200 different frames of EEG samples, each centred at a different post stimulus time ranging from +250 ms to +750 ms post-stimulus, and by calculating the mean coherence across all such frames for each stimulus category for each participant. The coherence value was averaged over time by allowing the centre point of this Hanning window to slide from +250 ms post stimulus to +750 ms post stimulus. In this way the coherence primarily reflects the EEG signal characteristics in the +250-+750 ms post stimulus window though some edge effects (due to the tapered edges of the Hanning window) in the -6ms to +250 ms post-stimulus region and the +750 to +1006 ms post-stimulus region.

The particular coherence metric used in this study was the event-related linear coherence (ERLCOH) which is a measure of the synchronization in activity between two electrode sites. This linear coherence value was computed for all electrode pairings using (1).

$$ERLCOH_{a,b}(f,t) = \frac{\sum_{k=1}^{n} F_k^a(f,t) F_k^b(f,t)^*}{\sqrt{\sum_{k=1}^{n} \left|F_k^a(f,t)\right|^2 \sum_{k=1}^{n} \left|F_k^b(f,t)\right|^2}} \qquad (1)$$

where n is the number of trials or epochs, $F_k^a(f,t)$ is the short time Fourier Transform of the Hanning windowed EEG samples for trial k on channel a at time t and frequency f and $F_k^a(f,t)^*$ is the complex conjugate of $F_k^a(f,t)$.

This cross channel coherence metric has a value in the range of 0 to 1(where a value of 0 represents the complete absence of synchronization between channels *a* and *b* at the frequency *f* during the time window centered on time *t* and a value of 1 represents perfect synchronization between these channels). The ERLCOH metric is a slight variation on the more commonly utilized event-related phase coherence (ERPCOH) in that the contribution of each epoch\trial is weighted according to the relative amplitude of the signal at each frequency whereas in the calculation of the ERPCOH metric all epochs\trials contribute equally to the coherence value.

As part of the process of calculating the ERLCOH, the inter-trial linear coherence (ITLC) as calculated by (2) is removed.

$$ITLC_a(f,t) = \frac{1}{n} \frac{\sum_{k=1}^{n} F_k^a(f,t)}{\sqrt{\frac{1}{n} \sum_{k=1}^{n} \left|F_k^a(f,t)\right|^2}} \qquad (2)$$

The ITLC is a *phase locking factor* (cf. Tallon-Baudry et al., 1996) which represents a measure of synchronization on a channel of the activity at time *t* and frequency *f* which is time locked to the experimental stimulus across the data trials. The subtraction of ITC during the calculation of ERLCOH should result in the *intrinsic* synchronization between the two electrode sites being reported.

ERLCOH was computed for 146 electrode pairings between 3 regions; frontal (F1, F2, FP1, FP2, AF3, AF4, FZ), temporal (T7, T8, TP7, TP8, TP9, TP10), and parietal (P1, P2, P3, P4, PO3, PO4, PZ, POZ). Pairings within each of the 3 regions were not considered. The linear coherence with ITC subtracted was computed for four frequencies; Theta 3 – 7 Hz, Lower alpha 7 – 9 Hz, Upper alpha 9 – 12.5 Hz, and Gamma 30 – 50 Hz.

Statistical Analyses

A series of two 2 (contextual background: detailed / white) x 2 (congruent / incongruent) x 3 (group: young, old, old declined) ANOVAs were conducted to examine recognition memory performance and reaction time performance on the visual paired associates task. A series of six 2 (contextual background: detailed / white) x 2 (time: early phase / late phase encoding) x 2 (hemisphere: right / left) x 3 (network: frontal-temporal, frontal-parietal, or temporal-parietal) x 3 (group: young, old, and old declined) mixed ANOVAs were run to examine coherence differences during encoding across each of the six frequency bands. Pearson's product moment correlations between memory performance (d') and coherence values were computed for each electrode pairing separately for stimuli presented on a detailed or white background during the early and late stages of encoding across each frequency band. Given the number of comparisons conducted in these analyses and the difficulties associated with quantifying differences across groups and conditions, the coherence-performance maps are interpreted with caution below.

Results

Recognition Memory

There was a main effect of group, F (2, 50) = 15.41, $p < .001$, with significant differences found between the young and old group, ($p < .001$) and between the young and old declined group ($p < .001$). Although there was no significant difference in overall recognition memory performance between the older control group and the older declined group (young M = 68.7, SD = 21.5; old M = 33, SD = 21.6, old decline M = 36.5, SD = 20.1), post-hoc analyses revealed one important difference between the two older adult groups. Specifically, older declined adults showed no memory benefits associated with context reinstatement, whereas compared with memory to congruent stimuli reinstated with a white background, older controls showed significantly better memory to congruent stimuli reinstated with a detailed background ($p < .05$; see Figure 2).

Insert Figure 2 around here

Recognition reaction time

There was a main effect of group, F (2, 50) = 28.65, $p < .001$, with younger adults (M = 1109.23, SD = 254.65) significantly faster and older adults (M = 1700.77, SD = 318.68) and older declined adults (M = 1641.71, SD = 389.22; $p < .001$ for both comparisons). No significant differences were observed between old and old declined groups.

Coherence

There was a main effect of network observed separately for each of the four frequencies (F(2, 96) = 66.32 - 424.95, p < .001), with frontal-parietal coherence being significantly greater than both frontal-temporal and temporal-parietal coherence across all frequencies and across all groups. A network x group interaction effect was observed for the upper alpha band, F(4, 96) = 5.08, p = .001, eta = 0.175, and the gamma band, F(4, 96) = 7.716, p < .001, eta = 0.243. When compared with both the old and old declined groups, younger adults generally had lower frontal-temporal and temporal-parietal coherence, but greater frontal-parietal coherence (see figure 3). Post-hoc analyses revealed a number of significant pairwise differences between the three groups: younger adults had lower frontal-temporal delta coherence when compared with older controls, F(1, 48) = 8.52, p < .005; younger adults had higher frontal-parietal upper alpha coherence when compared with older declined adults, F(1, 48) = 7.34, p < .01; and younger adults had higher frontal-parietal gamma coherence when compared with older controls, F(1, 48) = 4.65, p < .05, and older declined adults, F(1, 48) = 5.69, p < .05.

Insert Figure 3 around here

There was a time x network x group interaction effect for lower alpha, F(4, 96) = 4.177, p ¸.01, eta = 0.148 and upper alpha, F (4, 96) = 2.69, p < 0.05, eta = 0.1. For both frequency bands there was a trend for younger group to have lower frontal-temporal and temporal-parietal coherence during both the early and late phase of encoding when compared to both the older adult groups, with the most significant differences being observed in lower alpha in the temporal-parietal network ($p < .05$) . There was a consistent reduction in frontal-parietal coherence in the younger adult group from early to late phase encoding. Conversely, older adults showed an increase in frontal-parietal coherence from early to late phase encoding for both lower and upper alpha. The old declined group showed little or no change in frontal-parietal coherence from early to late stage encoding. Furthermore, for the old declined group coherence levels increased from early to late stage encoding for both the frontal-temporal and temporal-parietal networks but coherence in these same networks decreased for the old control group (see figure 4).

Insert Figure 4 around here

A context x network x group effect was also observed for lower alpha, $F(4, 96) = 3.50$, $p = 0.01$, eta = 0.127. Older declined adults showed a non-significant trend for higher coherence to stimuli presented on a white background relative to stimuli presented on a detailed background for both frontal-temporal and parietal-temporal networks, but a significant reverse trend was observed for frontal-parietal networks, $F(1, 48) = 9.34$, $p < .005$, with higher coherence to stimuli presented on a detailed background relative to stimuli presented on a white background (see figure 5). Similarly, younger adults tended to showed higher levels of coherence to stimuli with a detailed background across all three networks, but this effect was only significant for the frontal-parietal network, $F(1, 48) = 5.67$, $p < .05$. Old controls showed no significant differences in coherence level between stimuli presented on a detailed background versus on a white background.

Insert Figure 5 around here

In order to examine the relationship between coherence and performance in more detail, a series of Pearson's product moment correlations between d' and coherence values were computed for each electrode pairing separately for both phases and both stimuli types for each frequency band. This analysis allowed us to identify the coherence activations most strongly correlated with performance. The significant correlations are illustrated in the coherence maps in figure 6, 7, and 8 for the younger, older, and older declined groups, respectively. Relative to younger adults and older controls, better performance in the older cognitively declined group was associated with a greater number of negative coherence-performance relations.

Insert Figures 6 – 8 around here

Discussion

The current study examined EEG coherence and memory performance of young adults, normal older adults, and age- and education-matched older adults who perform 1SD below their peers on standardized memory tests. Consistent with our expectations, the young adult group performed better than both old and old declined groups on the visual paired associates task. Younger adults' recognition memory performance was significantly higher regardless of encoding context (detailed vs white background) and regardless of whether or not encoding context was reinstated during the recognition phase. Although the two older adult groups differed significantly on the Wechsler Logical Memory Scale, they did not differ significantly on overall memory performance in the visual paired associates task. However, while older declined adults showed no memory benefits associated with context reinstatement, older controls showed significantly better memory to congruent stimuli reinstated with a rich background.

We predicted group differences in coherence in response to task demands in lower and upper alpha and gamma bands, specifically, with lower levels of coherence expected in the older declined group. The current study revealed a number of significant coherence differences across the groups. The most prominent effect was higher coherence levels in younger adults relative to old and old declined adults in frontal-parietal networks, particularly for the gamma band. This was coupled with lower levels of coherence in younger adults relative to old and old declined adults in frontal-temporal and temporal-parietal networks for upper alpha, and gamma frequencies. This general trend was preserved regardless of manipulations of encoding context (i.e., white vs. detailed background) and stimulus repetition (early vs. late). Gamma is known to be involved in both perceptual binding and learning processes (Gruber, et al., 2004; Gruber, Muller, & Keil, 2002; Miltner, Braun, Arnold, Witte, & Taub, 1999; Osipova, et al., 2006). Higher levels of frontal-parietal gamma coherence may thus be a critical marker of successful encoding in the current study, as younger adults showed both higher levels of frontal-parietal gamma coherence and better overall memory performance. This is consistent with research suggesting that frontal-parietal networks play a critical role in the processing of visual-spatial information (Coull, Frith, Frackowiak, & Grasby, 1996), and research reporting age-related declines in frontal-parietal network activity during spatial memory (Muller & Knight, 2002). It may be that higher levels of gamma coherence in frontal-parietal networks along with relative suppression of gamma coherence in temporal-parietal and frontal-temporal networks are a marker of more successful encoding. Notably, post-hoc correlation analysis in the full sample revealed a significant negative correlation between memory performance and gamma coherence for both the frontal-temporal and temporal-parietal pathways in the left hemisphere ($r = -.346$, $p < .01$, and $r = -.290$, $p < .05$, respectively); and a borderline negative correlation between right frontal-temporal gamma coherence and performance, $r = -.274$ $p = .052$.

Although some studies have reported reduced interhemispheric lower and upper alpha band coherence associated with normal ageing and age-related cognitive decline during rest (Anghinah et al., 2000; Locatelli et al., 1998), and during cognitive processing (Hogan et al., 2003), research with MCI patients has also revealed an increase in alpha coherence as working memory demands increase (Jiang and Zheng, 2006). While we hypothesized lower alpha coherence in the older declined adults, this effect was observed only in the frontal-parietal networks. In contrast, when compared with older controls and older declined adults, there was a trend for younger adults in the current study to show lower levels of low alpha and upper alpha in frontal-temporal and parietal-temporal networks. In light of previous research suggesting a role for lower alpha in task effort and difficulty (Gevins et al., 1997; Klimesch, 1999), and upper alpha in semantic processing (Klimesch, 1999), these results may suggest that younger adults were drawing more selectively on frontal-parietal connections to manage task demands and thus required less coherent synchronization in temporal networks.

We hypothesised that older cognitive declined adults would show a less significant coherence difference between context rich and context poor pairs during encoding, and a less significant coherence difference in response to repetition of stimuli, particularly in both the lower and upper alpha frequency bands, which are known to be sensitive to the effects of ageing and to be associated with both effortful attention and the processing of semantic information, respectively. Converse to our hypothesis, older declined adults showed the largest difference between context rich and context poor stimuli in lower alpha in the frontal-parietal network. Like younger adults, older declined adults showed higher parietal-temporal coherence to stimuli presented on a detailed background.

With the exception of the frontal-parietal lower alpha and upper alpha coherence, we did not find consistent evidence for a less significant coherence difference in response to repetition of stimuli in older declined relative to older controls and younger adults. Younger adults showed a reduction in lower alpha coherence in frontal-parietal networks from early to late phase encoding, suggesting that task demands were reducing over time for this group – a finding which is also consistent with research showing a reduction in coherence associated with skill development (Busk & Galbraith, 1975; Deeney et al., 2009). Conversely, older declined adults showed an increase in lower and upper alpha coherence from early to late stage encoding in both frontal-temporal and temporal-parietal networks, which may suggest that both task demands and semantic processing were increasing over time for this group. One possible explanation for this finding in light of research suggesting more retroactive interference in older adults (Ebert & Anderson, 2009), may be that stimulus discrimination and semantic demands were increasing over time as more stimuli were presented for encoding.

The current study also examined the relationship between coherence during the early and late stages of encoding and subsequent memory performance in the younger, older control, and older declined groups, respectively. Consistent with the HAROLD model of aging (Cabeza, 2002), we hypothesised that younger adults would activate a smaller functional network associated with better memory performance, whereas older cognitively declined adults would activate the largest set of coherence-performance relations associated with better memory performance. Our findings provided some provisional support for this hypothesis. However, in light of the number of comparisons conducted in this context, we draw attention here to the exploratory nature of our coherence-performance analysis and we interpret our findings with caution.

First, younger adults showed predominantly negative coherence-performance correlations for fronto-parietal electrode pairs. These correlations were found for the lower alpha band mainly during the late stage of encoding. In the gamma range, negative coherence-performance correlations were observed during the early stages of encoding for stimuli presented on a rich contextual background. This result may reflect more pruning of networks in high performing younger adults in the situation where there is a detailed background within which memory targets are embedded. However, for stimuli presented on a white background, a greater number of negative coherence-performance correlations were observed in the latter stages of encoding.

Normal older adults generally showed a smaller number of coherence-performance correlations than both young and old declined adults. They had a more incoherent pattern of positive and negative coherence-performance correlations, including more interhemispheric than fronto-parietal connections. This suggests that better memory in normal older adults may be achieved using a different pattern of coherence networking.

Older cognitively declined adults were again characterized by a larger number of mostly negative coherence-performance correlations. They showed negative coherence-performance correlations in parieto-temporal, fronto-temporal, and fronto-parietal networks. This finding supports the importance of inhibiting irrelevant connections to achieve a better memory performance. This seems to be particularly true for cognitively declined individuals for whom increased inhibitory control problems have been suggested (Hasher & May, 1999; Hasher et al., 1991; Hasher & Zachs, 1988). The pattern of more diffuse coherence-performance networking in older declined was also observed when analysis was collapsed across background and time factors.

Overall, these results suggest that younger adults, older adults and older declined adults show differential patterns of coherence responding to contextual manipulations and stimulus repetition during encoding, and that memory performance is optimized in these groups using different patterns of coherence networking. While further research is needed to clarify the utility of coherence-performance mapping as a method of gaining insight into the functional dynamics of diffuse synchronous activity in the brain, the current study offers some useful insights in relation to the effects of ageing on brain dynamics associated with memory and suggests that coherence analysis may be further used to understand the nature of both optimal and sub-optimal memory performance.

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Table 1. Means and standard deviations (SD) for performance on neuropsychological assessment tasks for young, old, and old decline adults.

	Young (N = 19)		Old (N = 17)		Old decline (N = 15)	
	Mean	SD	Mean	SD	Mean	SD
Education (years)	15.8	2.3	12.9	3.2	12.5	3.1
NART	19.0	6.9	18.8	10.4	19.1	8.0
Fluency	24.9	8.0	17.2	5.6	18.9	4.7
WRAT	47.1	3.7	45.4	6.5	45.3	6.8
Wechsler Memory Subscales						
(standardized z-scores)						
Logical memory	1.11	0.9	1.16	0.83	0.18	1.28
Faces	0.98	2.13	0.90	0.98	-0.31	0.87
Visual Reproduction	1.47	1.22	0.98	0.98	0.58	1.08

Figures

Figure 1. Sample figures used in the figure paired associates learning task.

Figure 2. Recognition memory performance in younger, older, and older declined adults.

Figure 3. Mean coherence levels for younger adults, older adults and older declined adults for Delta, Upper Alpha and Gamma bands across frontal-temporal (FT), frontal-parietal (FP), and temporal-parietal (TP) networks.

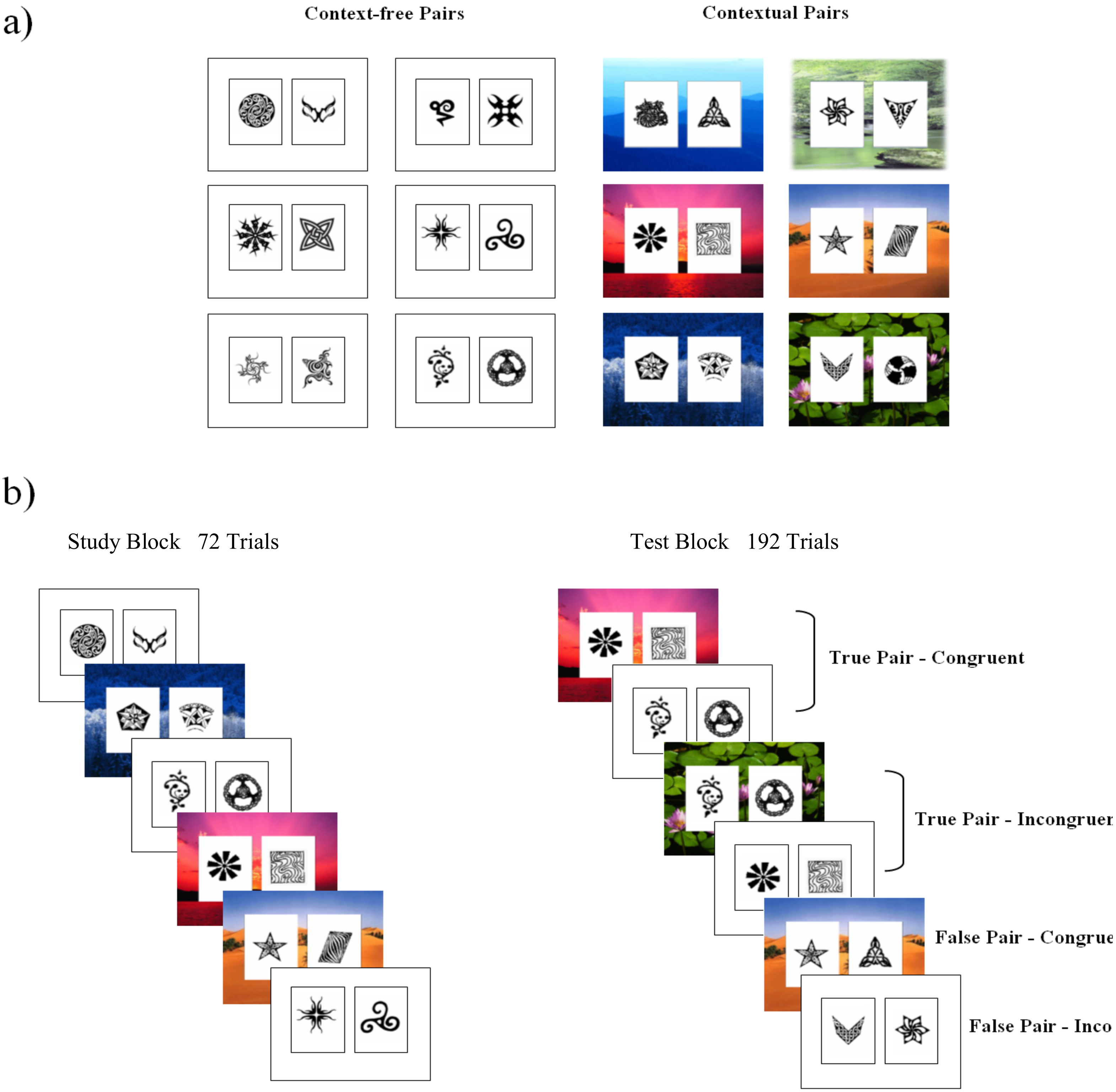
Figure 4. Mean coherence levels for Lower Alpha and Upper Alpha during both early and late phase encoding across frontal-temporal (FT), frontal-parietal (FP), and temporal-parietal (TP) networks for the three groups.

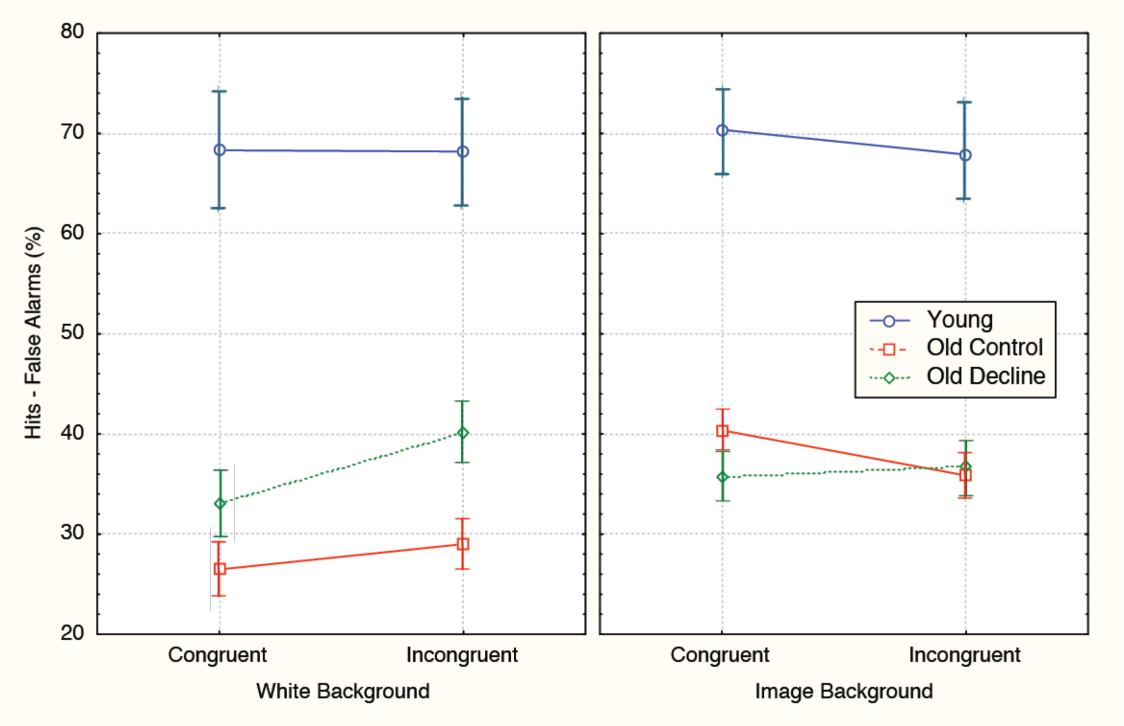
Figure 5. Mean coherence levels for Lower alpha for both a detailed background and white background across frontal-temporal, frontal-parietal, and temporal-parietal networks for younger adults, older adults and older declined adults.

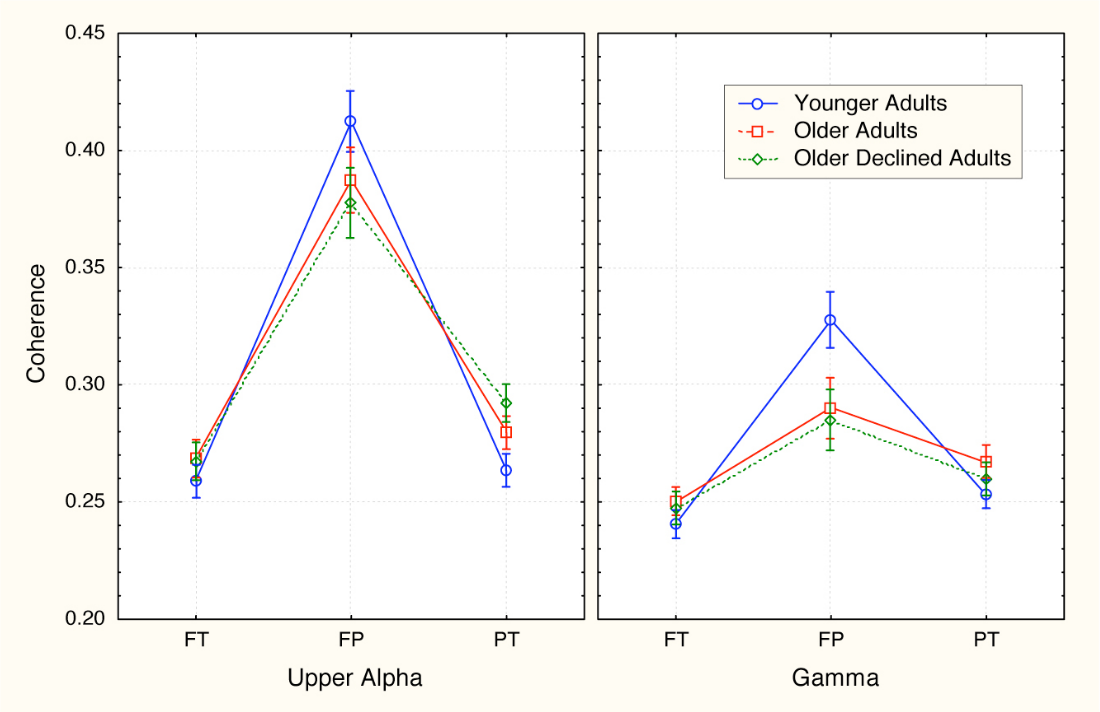
Figure 6. Younger adults coherence-performance maps for early and late phases of encoding, and for pairs with and without background images. Red lines indicate positive correlations, and blue lines indicate negative correlations (thin lines = $p < .05$ and thick lines = $p < .001$).

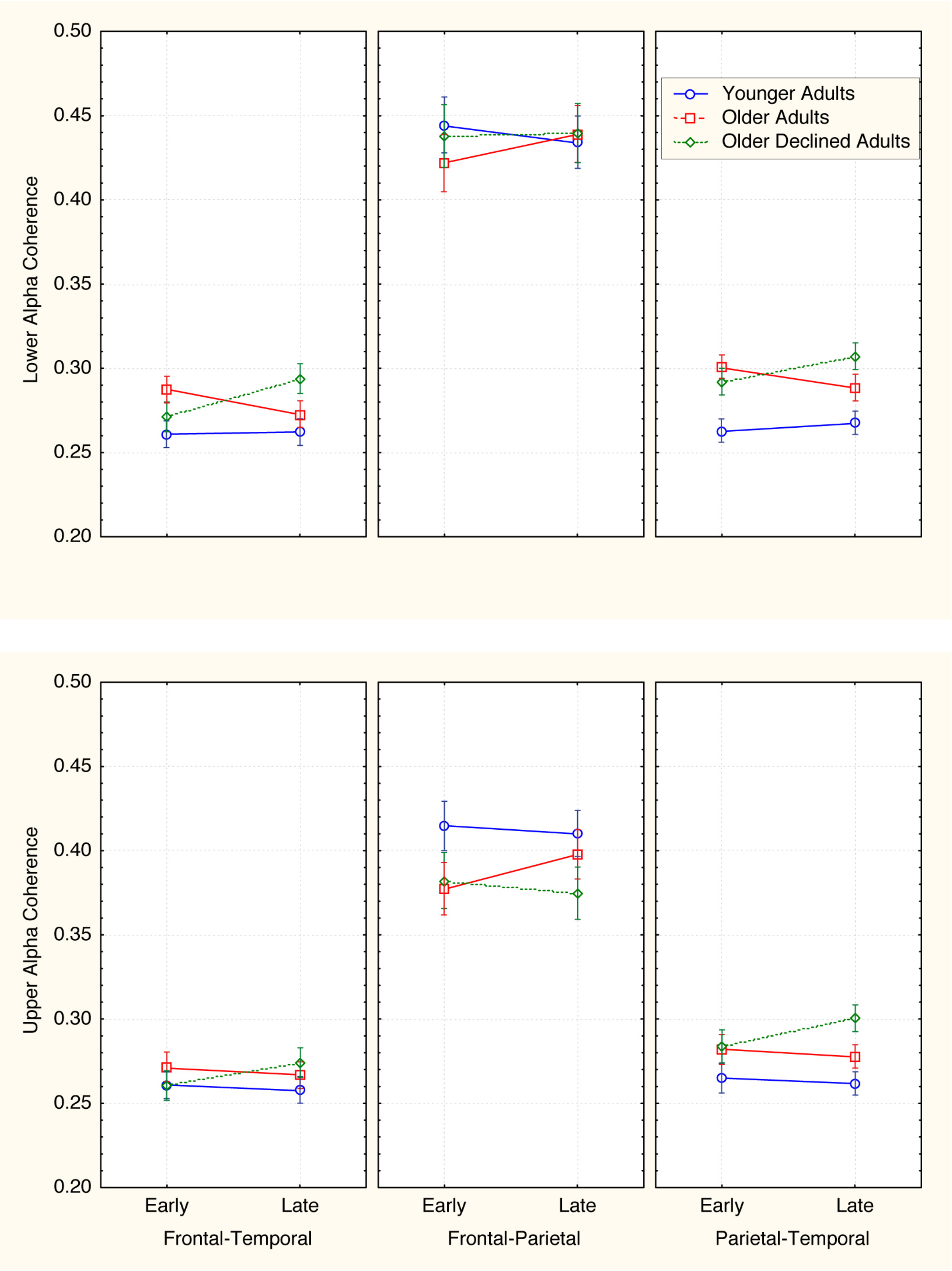
Figure 7. Older adults coherence-performance maps for early and late phases of encoding, and for pairs with and without background images. Red lines indicate positive correlations, and blue lines indicate negative correlations (thin lines = $p < .05$ and thick lines = $p < .001$).

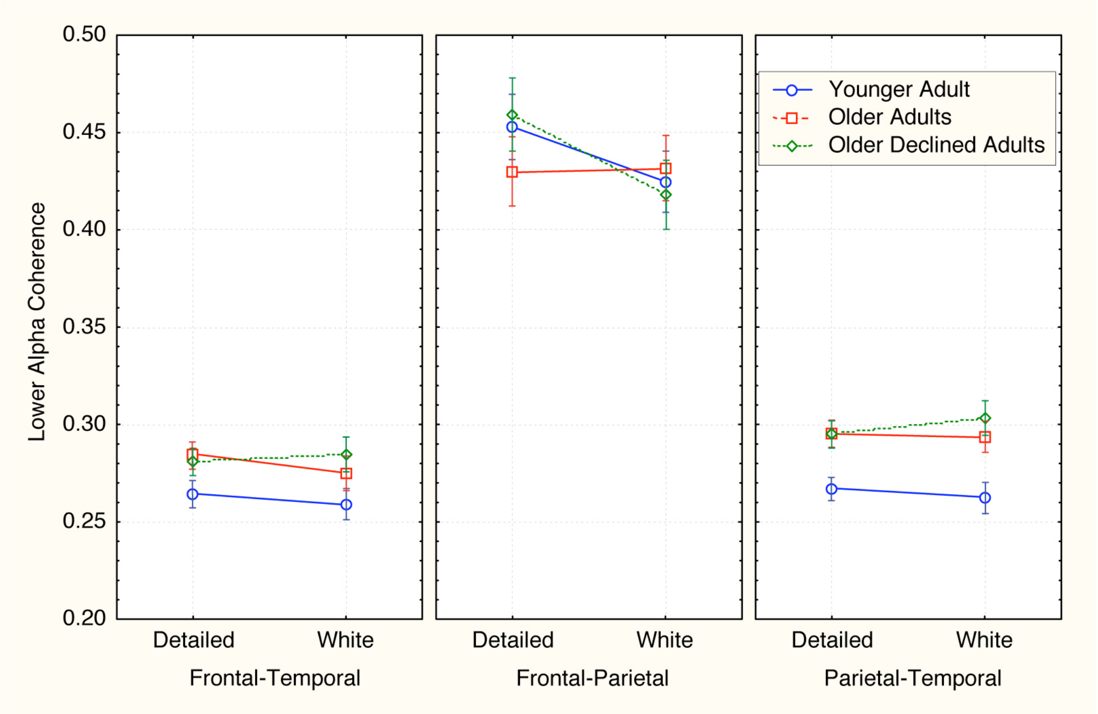
Figure 8. Older declined adults coherence-performance maps for early and late phases of encoding, and for pairs with and without background images. Red lines indicate positive correlations, and blue lines indicate negative correlations (thin lines = $p < .05$ and thick lines = $p < .001$).


a)
Context-free Pairs
Contextual Pairs
b)
Study Block 72 Trials
Test Block 192 Trials
True Pair - Congruent
True Pair - Incongruen
False Pair - Congrue
False Pair - Inco

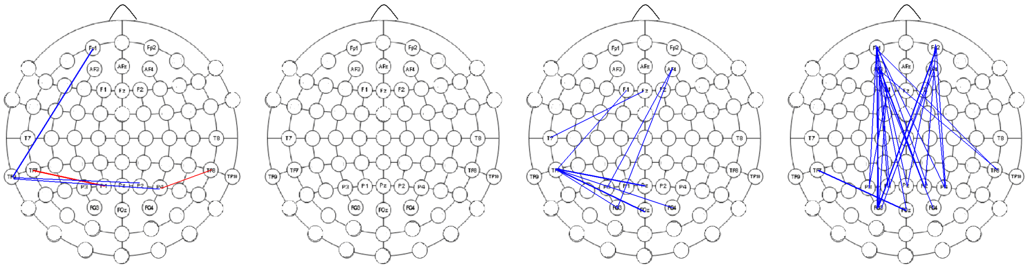

80
70
60
50
40
30
20
Hits - False Alarms (%)
Congruent
Incongruent
White Background
Congruent
Incongruent
Image Background
Young
Old Control
Old Decline


0.45
0.40
0.35
0.30
0.25
0.20
Coherence
FT
FP
PT
Upper Alpha
Gamma
Younger Adults
Older Adults
Older Declined Adults


0.50
0.45
0.40
0.35
0.30
0.25
0.20
Lower Alpha Coherence
Younger Adults
Older Adults
Older Declined Adults
Upper Alpha Coherence
Early
Late
Frontal-Temporal
Frontal-Parietal
Parietal-Temporal

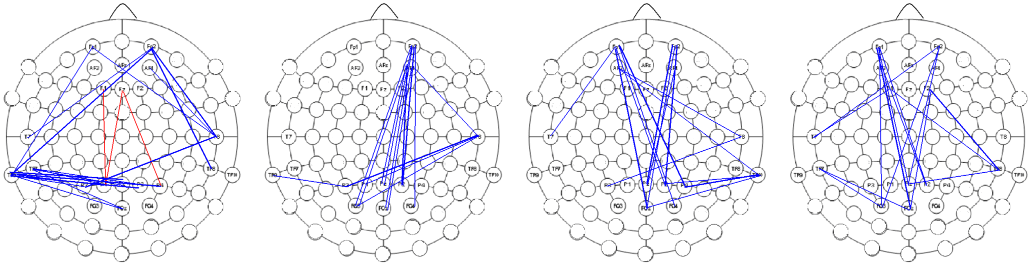

Lower Alpha Coherence
0.50
0.45
0.40
0.35
0.30
0.25
0.20
Younger Adult
Older Adults
Older Declined Adults
Detailed
White
Frontal-Temporal
Detailed
White
Frontal-Parietal
Detailed
White
Parietal-Temporal

Young – Early – Image Background



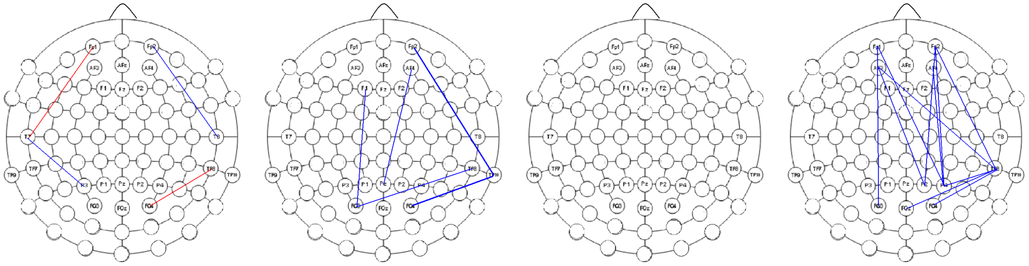
Theta Lower Alpha Upper Alpha Gamma

Young – Late - Image Background



Theta Lower Alpha Upper Alpha Gamma

Young – Early - No Background



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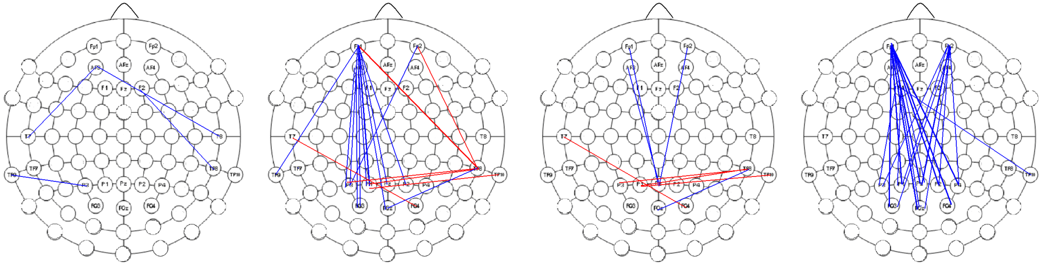
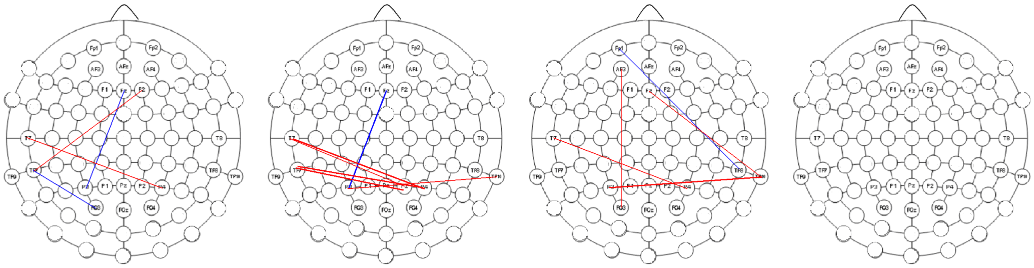
Young – Late - No Background



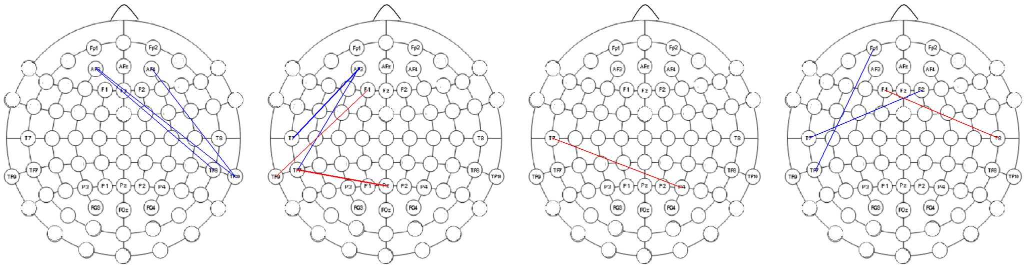
Theta Lower Alpha Upper Alpha Gamma

Old – Early– Image Background



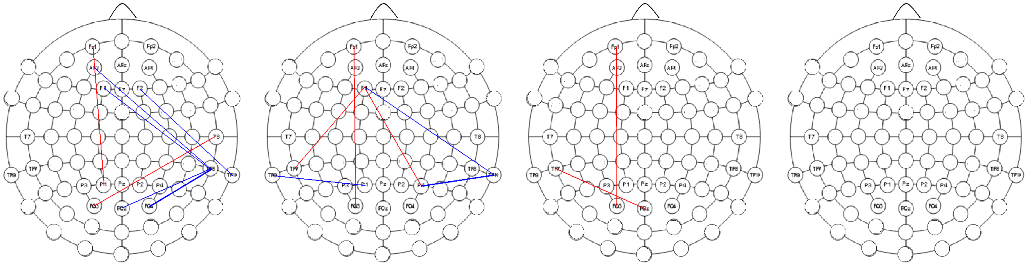
Theta Lower Alpha Upper Alpha Gamma

Old - Late – Image Background



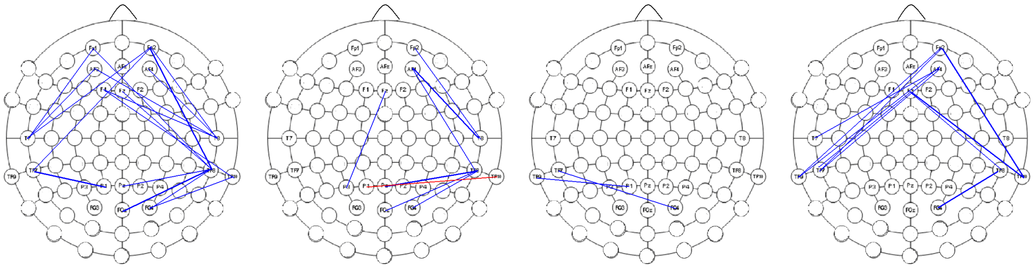
Theta Lower Alpha Upper Alpha Gamma

Old – Early - No Background



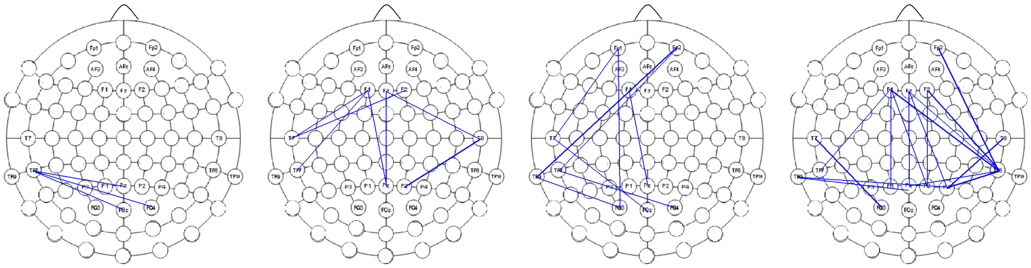
Theta Lower Alpha Upper Alpha Gamma

Old – Late - No Background



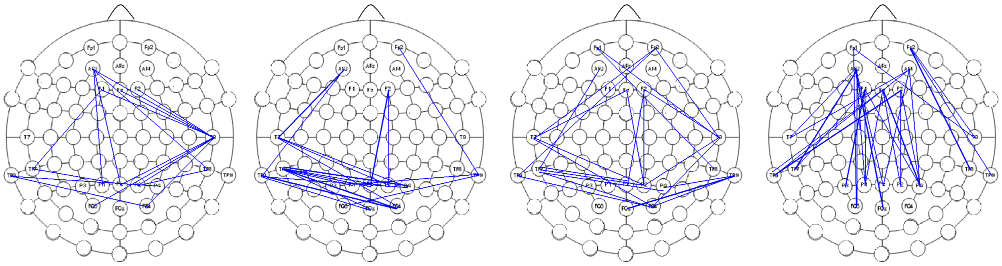
Theta Lower Alpha Upper Alpha Gamma

Old Cognitive Decline – Early – Image Background



Theta Lower Alpha Upper Alpha Gamma

Old Cognitive Decline – Late – Image Background



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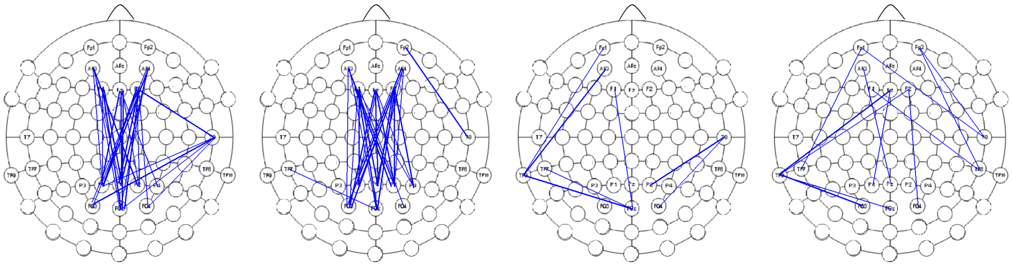

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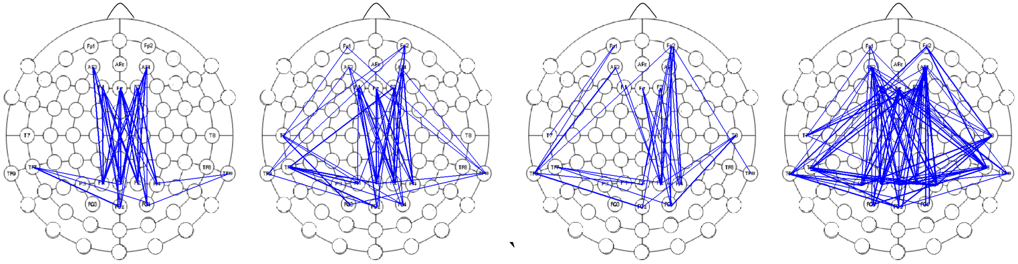

Theta Lower Alpha Upper Alpha Gamma